

# ZOOGEOGRAPHY OF GREAT BASIN BUTTERFLIES: PATTERNS OF DISTRIBUTION AND DIFFERENTIATION

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**ABSTRACT.**—The butterflies of the Great Basin exhibit general patterns of distribution and speciation similar to those found for other taxa, particularly birds. Two major centers of infraspecific differentiation and coinciding distribution limits of taxa are identified, each with three subregions. Great Basin butterflies are characterized by pallidity and substantial endemism below the species level.

The Great Basin of western North America is a huge area, nearly 520,000 square kilometers, of largely internal drainage between the Rocky Mountains to the east and the Sierra Nevada to the west. It includes Utah west of the Wasatch Plateau, extreme southwestern Idaho and southeastern Oregon, California east of the Sierra Nevada, and nearly all of Nevada (Fig. 1). Elevations range from 1,000-m lowlands dominated by sagebrush (*Artemisia*) and saltbush (*Atriplex*) to numerous, mostly north-south oriented mountain ranges which may exceed 3,000 m. These mountain ranges, most of which are forested only at the higher elevations, constitute islands of boreal habitat. Lowland wet areas are similarly islandlike. The area is largely uninhabited by humans and is relatively undisturbed except for livestock grazing which has had substantial impact on the composition of the vegetation, especially at lower elevations (e.g., Rogers 1982, Thomas 1983).

Studies of the distribution and biogeography of Great Basin biota have dealt largely with vertebrates (e.g., Behle 1963, 1978, Brown 1971, 1978, Grayson 1982, 1983, Johnson 1975, 1978, Smith 1978) and plants (e.g., Billings 1978, Harper et al. 1978). Here we present information on the distribution of Great Basin butterflies, paying particular attention to the distributional limits of species, subspecies, and well-differentiated segregates, and to centers of infraspecific differentiation. Additionally, we discuss the role of "island" effects in shaping local species richness.

## MATERIALS AND METHODS

Distribution maps for butterfly taxa and other distinct phenotypes occurring within and on the margins of the Great Basin were constructed from a variety of sources. Nevada data are drawn primarily from the collections and field notes at the Nevada State Museum, Carson City, the senior author's personal collection, and collections made by the Center for Conservation Biology at Stanford University. Eastern California data were obtained from the notes and collections of a number of private collectors. Southern Oregon records are from Dornfeld (1980), and Rocky Mountain and eastern Great Basin records are from Ferris and Brown (1981). Some Sierra Nevada data were obtained from Shapiro et al. (1979) and the collections of the Nevada State Museum. Numerous other literature sources were consulted.

The maps thus prepared were examined to determine patterns of distribution within the Great Basin and adjacent areas. Attention was paid to the absence or presence of species within the Great Basin and the extent of their apparent distributions and differentiation in the Great Basin.

## TAXA AND DISTRIBUTION

The 155 butterfly species occurring in the Great Basin include some 240 subspecies and well-differentiated segregates. More than half the species are geographically polytypic in this and adjacent regions, including the Rocky

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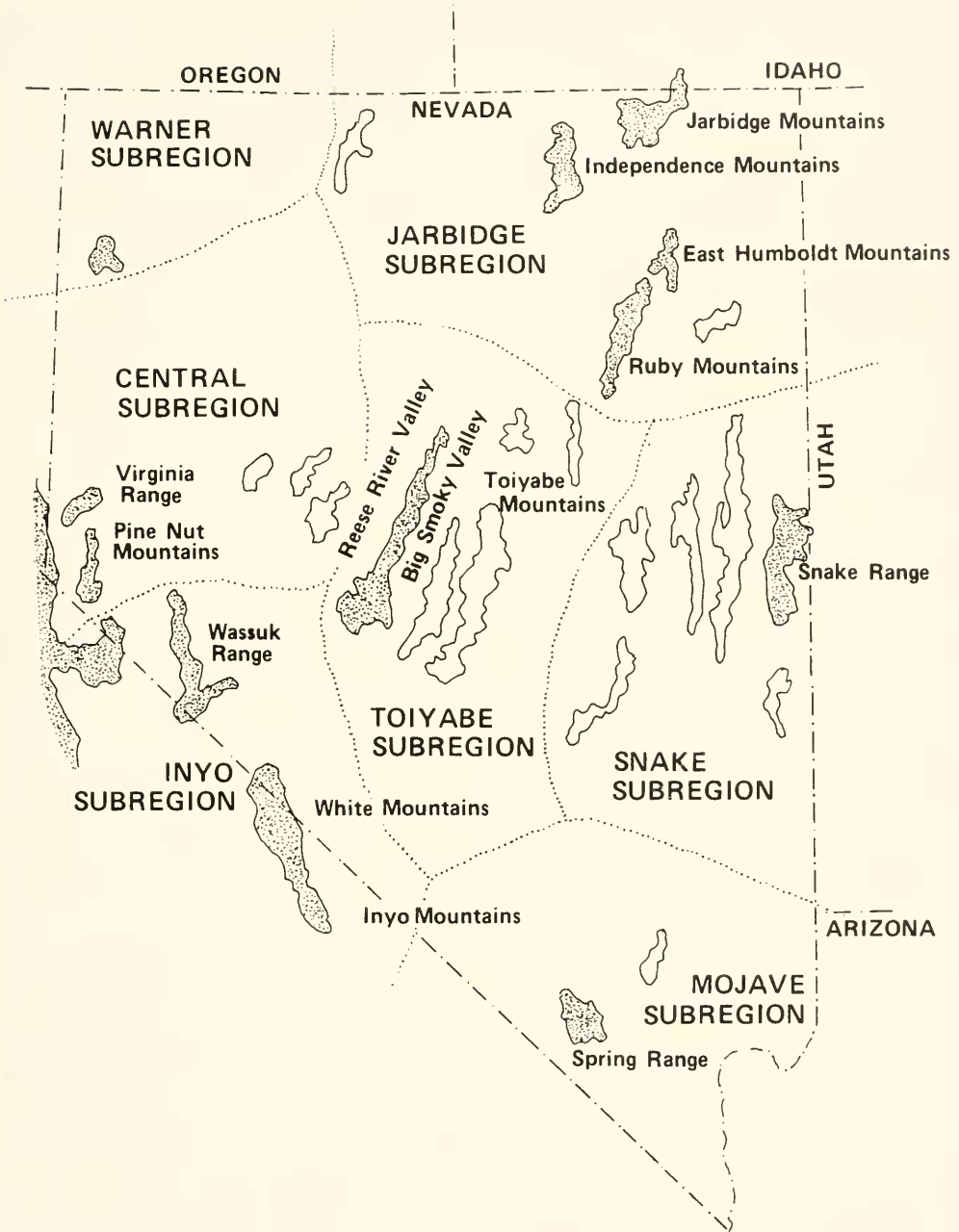


Fig. 1. The Great Basin showing subregions and locations mentioned in the text.

Mountains and Sierra Nevada. No species are endemic to the Great Basin, consistent with previous findings for birds (Behle 1963). About 50 subspecies and other well-differentiated infraspecific segregates (distinct groups of phenotypically similar, but unnamed, populations) of butterflies, however, are re-

stricted to the Great Basin. A number of additional groups of populations within the region show some measurable differentiation. The distributions of these taxa and segregates by geographic affinities are summarized in Table 1.

Nearly 90% of all Great Basin butterfly species are also found in the Rocky Mountains.

TABLE 1. Affinities of the Great Basin butterfly fauna. Taxa include subspecies and distinct unnamed segregates.

	Species	Taxa
Sierra Nevada	8 (5.2%)	35 (14.5%)
Rocky Mountain	30 (19.3%)	67 (27.8%)
Widespread (including Sierra Nevada and Rocky Mountains)	99 (63.8%)	48 (19.9%)
Endemic	0 (0.0%)	52 (21.6%)
Southern	15 (9.7%)	29 (12.0%)
Northern	3 (1.9%)	10 (4.1%)
TOTAL NUMBER	155	241

Only about two-thirds of the Great Basin butterfly species occur in the Sierra Nevada. When considering truly widespread Great Basin taxa as opposed to those occurring merely on the margins, Great Basin butterflies shared with the Rocky Mountains outnumber those shared with the Sierra Nevada by about three to one.

Great Basin butterflies are made up of several distinct groups:

1. A large number of relatively widespread species which occur in the Great Basin as endemic subspecies or segregates (many of which represent the species' most pallid phenotype). This in itself identifies the Great Basin as a distinct region of differentiation for butterflies.

2. A group of widespread species which occur throughout much of the western portion of the continent. The majority of these species show little or no regional differentiation.

3. A number of desert taxa extending into the Great Basin from the south, reaching their northern limit there and either occurring only along the southern fringe of the basin or ranging further north as permanent populations, seasonal populations, or stray individuals. Many other species occur just south of the Great Basin in extreme southern Nevada and southwestern Utah (e.g., Austin and Austin 1980).

4. And, finally, there are a few butterflies of mainly northern affinity that range south into the Great Basin. Nearly all of these are limited to the northern portion of the Great Basin.

The Great Basin butterfly fauna is characterized not only by the presence of numerous endemic phenotypes but by the restricted distribution or conspicuous absence of certain taxa. The borders of the Great Basin addition-

TABLE 2. Widespread Rocky Mountain and Sierra Nevada butterfly species absent or nearly so from the Great Basin.

<i>Epargyreus clarus</i>
<i>Thorybes pylades</i>
<i>Thorybes mexicana</i>
<i>Erynnis pacuvius</i>
<i>Pyrgus ruralis</i>
<i>Polites souora</i>
<i>Euphyes vestris</i>
<i>Amblyscirtes vialis</i>
<i>Parnassius clodius</i>
<i>Lycaena mariposa</i>
<i>Plebejus idas</i>
<i>Plebejus franklini</i>
<i>Speyeria hydaspes</i>
<i>Boloria epithore</i>
<i>Chlosyne palla</i>
<i>Polygonia faunus</i>

ally provide range limits for a large number of species. An indication of this can be seen in Scott's (1986) "spaghetti diagram" of the entire North American fauna. Some, particularly desert, species are apparently prevented from entering the region by climatic factors either directly limiting the butterflies or their larval host plants. Severity of Great Basin winters is probably one such factor, but this does not explain all absences. Many other species might be expected at specific locations within the Great Basin where suitable conditions seem to exist.

At least 16 species that occur on the very fringes of the Great Basin (Table 2) are widely distributed in the Rocky Mountains, west to Oregon and south through the Cascades to the Sierra Nevada. Other species exhibit a similar northern distribution pattern but do not occur in either the Rockies or Sierra Nevada. These absences from the Great Basin may be due to interacting factors that include climate, absence or paucity of suitable habitats and host plants, and the inability of these species to disperse across expanses of desert (i.e., Holdren and Ehrlich 1982). Still another possibility is that some species once occurred in the Great Basin but have been extirpated by increasing aridity and concomitant habitat constriction following the Pleistocene (e.g., Wells 1983). Noteworthy, however, is that few species show disjunct distribution patterns suspected to be relictual. *Pholisora catullus*, *Speyeria egleis*, *Lycaena nivalis*, and *L. editha* are found in the Toiyabe Mountains of Lander and Nye counties, Nevada. The clos-

TABLE 3. Distribution of Great Basin endemic butterflies by region.<sup>1</sup>

## EASTERN REGION

## Jarbidge

*Ochlodes sylvanoides bonnetilla*  
 \**Lycaena editha nevadensis*  
 \**Euphilotes rita mattonii*  
 \**Speyeria atlantis greyi*  
 \**Speyeria atlantis elko*  
*Speyeria mormonia artonis*  
*Phycodes campestris seg.*  
*Euphydryas colon nevadensis*

## Snake

*Polites sabuleti seg.*  
*Satyrium saepium seg.*  
 \**Incisalia augustus (?) seg.*  
 \**Euphilotes battoides seg.*

## Toiyabe

*Polites sabuleti seg.*  
*Papilio indra nevadensis*  
 \**Speyeria egleis toiyabe*  
 \**Cercyonis oetus pallescens*

## Widespread

*Euphydryas editha lehmani*  
*Euphydryas editha koreti*

## WESTERN REGION

## Inyo

*Thorybes mexicana blanca*  
 \**Hesperia miramae seg.*  
 \**Polites sabuleti seg.*  
*Lycaena rubidus seg.*  
*Euphilotes mojave langstoni*  
 \**Plebejus icarioides seg.*  
 \**Plebejus saepiolus seg.*  
*Coonympha ochraceae mono*  
 \**Cercyonis pegala wheeleri*  
*Neominois ridingsii seg.*

## Central

\**Pseudocopaeodes eunus seg.*  
 \**Polites sabuleti genoa*  
 \**Euphilotes rita seg.*  
*Speyeria zerene malcolmi*  
*Speyeria callippe nevadensis*  
*Euphydryas editha monoensis*  
 \**Cercyonis pegala seg.*

## Warner

*Polites sabuleti seg.*  
 \**Polites sabuleti seg.*  
 \**Pieris napi seg.*  
*Lycaena rubidus rubidus*  
*Cercyonis pegala stephensi*

## Widespread

*Hesperia uncas macswaini*

## WIDESPREAD IN GREAT BASIN

*Colas alexandra edwardsii*  
*Lycaena arota virginensis*  
*Mitoura siva chalcosiva*  
*Euphilotes battoides baueri*  
*Euphilotes rita pallescens*  
*Glaucopsyche pius nevada*  
*Speyeria nokomis apacheana*

Table 3 continued.

*Speyeria zerene gunderi*  
*Limnitis archippus lahontani*  
*Cercyonis sthenele paulus*  
*Neominois ridingsii stretchii*

<sup>1</sup>Here and in subsequent tables, seg. (segregate) is used to denote distinct sets of phenotypically similar populations which are as yet unnamed

\*Narrowly distributed taxon

est extant populations apparently are now well to the north. *Papilio indra*, in addition, exists as a relatively isolated endemic subspecies in the same general area, and *Plebejus lupini* occurs as widely scattered populations across central Nevada. Several of these same species also extend into montane areas south of the Sierra Nevada cordillera (Emmel and Emmel 1973), indicating an ability to survive in more xeric conditions than those at their distribution centers.

## CENTERS OF DIFFERENTIATION

A number of Great Basin species are comparatively unvarying in phenotype over a broad area from the Rocky Mountains or eastward, west to the Sierra Nevada or beyond. Others exhibit considerable regional differentiation and may include one or more phenotypes restricted to the Great Basin. The large number of phenotypic endemics suggests that the Great Basin is at least a moderately active area of infraspecific differentiation. Examination of the distributions of subspecies and segregates of polytypic species in the Great Basin and adjacent butterfly faunas shows rather well defined distribution patterns suggesting "centers of differentiation." Similar to Behle's (1963) findings for birds, these centers are bounded by areas where numerous range limits coincide, further suggesting that the Great Basin consists of definable biogeographical units (Fig. 1, Table 3). These regions generally coincide with distributional limits or more widespread butterfly taxa and are strikingly similar to distributional centers found for birds (Behle 1963, 1978).

## Eastern Region

The Great Basin may be viewed as two distinct centers of butterfly distribution and differentiation (Fig. 1). The first is the Eastern Region bounded by the Wasatch Front in the east, to and including the Reese River Valley



and from the northern limits of the Mojave Desert in the south, north to southern Idaho and southeastern Oregon. The area includes the Pleistocene Lake Bonneville basin, eastern portions of the Pleistocene Lake Lahontan basin, the Ruby group of drainages, and the southern portion of the Snake River drainage group (see Smith 1978). This region is comprised of three subregions: (1) the Jarbidge Subregion (southern Snake, northern Bonneville, and northeastern Lahontan drainages)—including the area north of the Humboldt River to central Humboldt County in Nevada, adjacent southeastern Oregon, southern Idaho, and northwestern Utah; (2) the Snake Subregion (Ruby and southern Bonneville drainages)—including the remainder of the Great Basin along the eastern border of Nevada and western Utah; and (3) the Toiyabe Subregion (southeastern Lahontan drainage)—including the central portion of Nevada. The Eastern Region loosely corresponds to Behle's (1963) concept; however, he did not subdivide the region, and he included more of Idaho.

The most clearly defined center of differentiation in the Eastern Region is the Jarbidge Subregion. Three subspecies are narrowly restricted to the Jarbidge and Independence ranges and another to the Ruby and East Humboldt ranges (Table 3). Three other subspecies and one segregate are distributed more broadly in the subregion. The Snake Subregion has two apparent narrowly distributed segregates in the vicinity of the Snake Range and two others more widely distributed. The Toiyabe Subregion has two narrowly distributed subspecies and one subspecies and one segregate more widespread. Two other endemic Great Basin subspecies are more widely distributed in the Eastern Region, ranging into two or more of the subregions.

#### Western Region

This region includes the area from the western edge of the Eastern Region (defined above) to the east slope of the Sierra Nevada, north from the Mojave Desert to south central Oregon (Fig. 1). The area includes the western portion of the Pleistocene Lake Lahontan basin and the southern Oregon Lakes drainage group (Smith 1978). Again three subregions may be discriminated: (1) the Inyo

Subregion (southwestern Lahontan basin)—including the White Mountains and adjacent areas, Wassuk and Sweetwater mountains, and adjacent east slope of the Sierra Nevada of Nevada and California; (2) the Warner Subregion (southern Oregon Lakes drainage)—including northeastern California, northwestern Nevada, and south central Oregon; and (3) the Central Subregion (west central and northwestern Lahontan basin)—the area between the above (Fig. 2). Behle (1963) excluded, but later included (Behle 1978), the Inyo and Warner subregions in the Western Region and discussed them as separate biogeographic entities (see also Miller 1941, Johnson 1970).

The Inyo Subregion is the most well defined center of butterfly differentiation in the Western Region (Table 3). Speciation in this area is greatest in the White Mountains where at least one endemic subspecies and four endemic segregates are recognizable. Another subspecies is restricted to the Owens Valley. An additional four subspecies are more widely distributed in the subregion.

The Warner Subregion has at least two endemic subspecies and three endemic segregates. The Central Subregion is geographically broad and not sharply defined. There are three restricted segregates and one restricted subspecies and three more widely ranging subspecies, some of which extend for varying distances into the Inyo and/or Warner subregions. One additional subspecies is relatively widespread throughout the Western Region.

Finally, 11 endemic Great Basin subspecies occur in at least one (usually more) subregion of both the Eastern and Western regions.

#### SPECIATION PHENOMENA

Zones in which subspecies or segregates interface are found throughout the Great Basin. Some, however, emerge prominently as areas of intergradation for a wide variety of species when distribution and differentiation patterns are examined. Similar phenomena were identified and discussed for birds by Johnson (1978). Here we follow that presentation for butterflies. Areas where speciation appears to be less obvious coincidentally have been less well studied. But, while further knowledge may somewhat alter the details, the overall definition of these zones and the

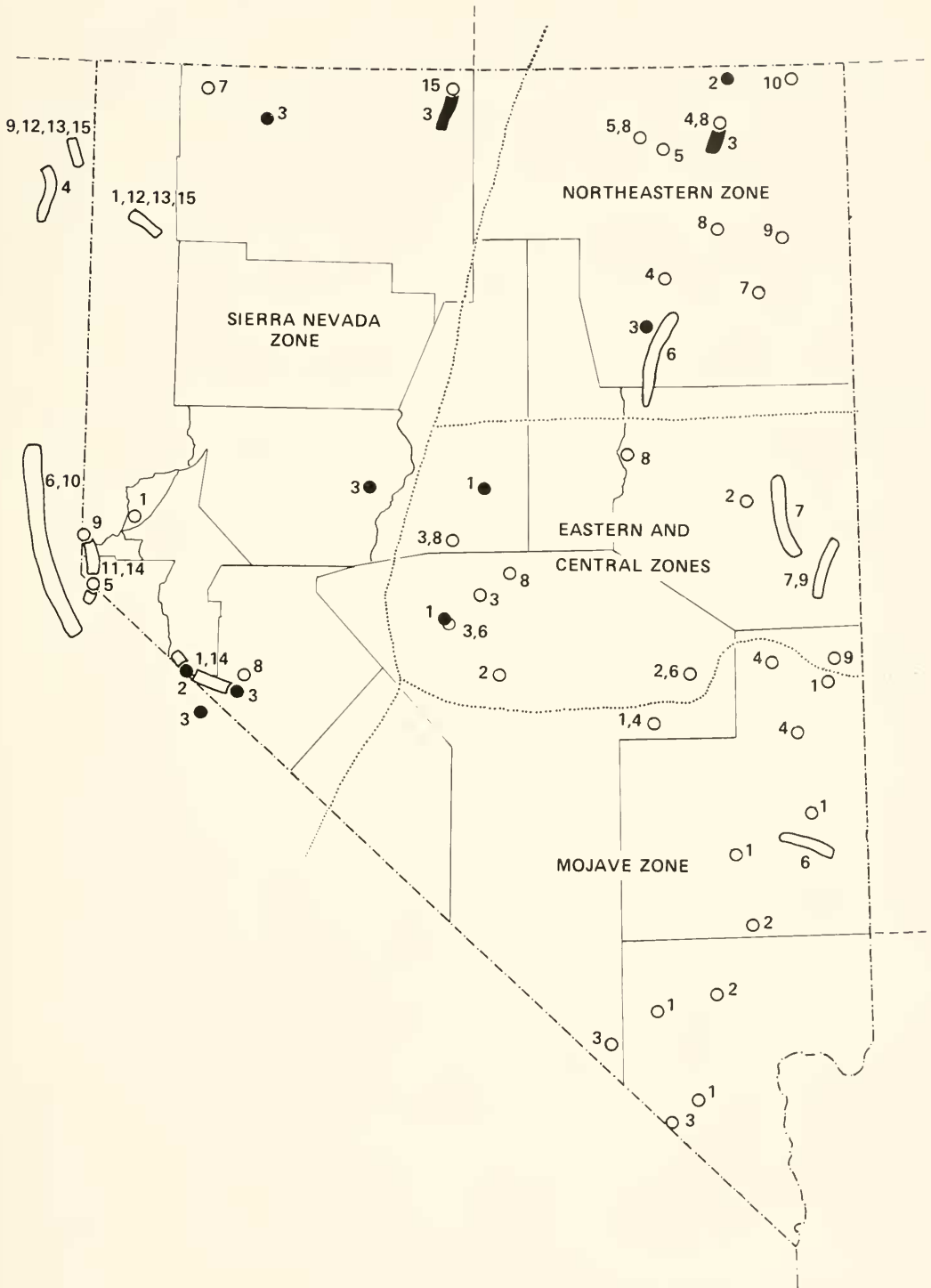


Fig. 2. Areas of interaction among Great Basin butterflies. Numbers refer to species pairs in Table 4 (Sierra Nevada), Table 5 (northeastern Nevada), Table 6 (eastern and central Nevada), and Table 7 (Mojave). Solid symbols refer to interspecific hybridization; open symbols refer to intraspecific intergradation.

interactions described appear to be sound. Note also that there are some recent records of shifts in the ranges of birds in these same geographic areas of interaction (e.g., Johnson and Johnson 1985).

Pairs of related taxa or segregates are categorized by the type and degree of interaction. In the following sections we discuss areas where subspecies or segregates and closely related species come into contact. A number of closely related species hybridize in these areas. Intergradations between subspecies or segregates include primary intergradations (those between phenotypically similar subspecies or segregates such as those along a cline) and secondary intergradations (those between phenotypically more dissimilar subspecies segregates such as "internal contact" of those from distant points on a ring or *rassenkreis*). Also, in the same geographic areas some species and subspecies (or segregates) exhibit range disjunctions. These zones of allopatry may be geographically wide (such as across the Lahontan Basin) or narrow (between adjacent mountain ranges). Taxa also can be separated by elevation (high and low populations in the same mountain range) or time (flying at different seasons).

#### Sierra Nevada Zone

Perhaps the most striking element of Great Basin biogeography is the predominance of Rocky Mountain and closely related Great Basin taxa in relative proximity to the east slope of the Sierra Nevada. The occurrence of Sierra Nevada biotic elements east into the Great Basin, conversely, is rare (Behle 1978, Harper et al. 1978, Johnson 1978, Tanner 1978). For instance, in the Snake Range, centrally located in the Great Basin, 54% of 86 species are represented by subspecies that are either shared with the Rocky Mountains or are Great Basin subspecies or segregates most similar to Rocky Mountain taxa. Only 3% of species are of Sierra Nevada affinity. In the Toiyabe Range in the west central Great Basin, 50% of 92 species have Rocky Mountain affinities, while 4% are similar to Sierra Nevada taxa. And, in the White Mountains, just several dozen kilometers from and in direct sight of the Sierra Nevada crest, 34% of 79 species are most similar to Rocky Mountain taxa, and only 17% are of Sierra Nevada affinity.

The east slope of the Sierra Nevada and the adjacent western Great Basin, as a consequence, might be expected to be an area of vigorous interaction among distinguishable butterfly taxa which may have only recently come into contact. This is the single most active area of intergradation for Great Basin birds (Johnson 1978, Johnson and Johnson 1985), and the same appears to be true for butterflies (Table 4). These interactions include many species and involve a wide variety of types and degrees of differentiation and/or disjunct distributions within this geographic area (Fig. 2).

Geographic areas of contact within the Sierra Nevada Zone are generally narrow. Sierran *Speyeria zereue zereue* and a western Great Basin subspecies, *S. z. malcolmi*, for example, intergrade (a primary intergradation) only in the vicinity of Carson City (Moeck 1957, Grey and Moeck 1962). The more widespread Great Basin subspecies, *S. z. gunderi*, intergrades with *S. z. conchylhiatus* in the Granite and Warner mountains on the northern Nevada-California border (a secondary intergradation between Rocky Mountain and Sierra Nevada subspecies [Grey and Moeck 1962, Grey 1972]). Two *Speyeria calippe* phenotypes (*S. c. nevadensis* and *S. c. near semivirida*) intergrade in this same area. A population of *Neominois ridingsii*, apparently intermediate between *N. r. stretchii* and an as yet undescribed Sierra Nevada segregate, occurs here as well. *Euphydryas anicia wheeleri* and *E. chalcedona macglashanii* produce an apparently intermediate population in the Sweetwater Mountains (Murphy and Ehrlich 1983), while *E. anicia macyi* and *E. a. veazieae* intergrade across a broad area along the Oregon and Nevada border.

The extreme western Great Basin ranges additionally have some Sierra Nevada-derived taxa or segregates which are phenotypically distinct. *Thorybes mexicana blanca* of the White, Wassuk, and Sweetwater mountains and undescribed *Hesperia mirianae* and *Lycena rubidus* segregates restricted to the White Mountains are examples of populations closely related to Sierra Nevada taxa. The latter appears related to the Sierran subspecies, *L. r. monachensis*, and is replaced elsewhere in the Great Basin by the widespread *L. r. sirius*.

Some species or subspecies (or segregate)

TABLE 4. Taxa pairs of butterflies that show various speciation phenomena in the western Great Basin/east slope Sierra Nevada region (most widespread Great Basin taxon listed before Sierra Nevada or other taxon).

NARROW ZONE OF SYMPATRY AND INTERSPECIFIC HYBRIDIZATION

1. *Mitoura siva chalcosiva* and *M. nelsoni nelsoni*
2. *Euphydryas anicia wheeleri* and *E. chalcedona macglashanii*
3. *Limenitis weidemeyerii latifascia* and *L. lorquini*

NARROW ZONE OF SYMPATRY AND INTERGRADATION BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

4. *Hesperia comma harpalus* and *H. comma yosemite*
5. *Anthocharis sara thoosa* and *A. s. stella*
6. *Lycacna arota virginensis* and *L. a. arota*
7. *Lycacna rubidus sirius* and *L. r. rubidus*
8. *Callophrys sheridanii comstocki* and *C. s. lemberti*
9. *Euphilotes battoides glaucon* and *E. b. battoides* or *E. b. intermedia*
10. *Plebejus icarioides fulla* and *P. i. icarioides*
11. *Speyeria zerene malcolmi* and *S. z. zerene*
12. *Speyeria zerene gunderi* and *S. z. conchyltatus*
13. *Speyeria callippe nevadensis* and *S. e. semivirida*
14. *Phyciodes campestris campestris* and *P. c. montana*
15. *Neominois ridingsii stretchii* and *N. ridingsii* seg.

NARROW ZONE OF ALLOPATRY BETWEEN CLOSELY RELATED SPECIES:

16. *Chlosyne acastus acastus* and *C. palla* seg.
17. *Coenonympha ochracea mono* and *C. ampelos ampelos*

NARROW ZONE OF ALLOPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

18. *Thorybes mexicana blanca* and *T. mexicana nevada*
19. *Hesperia miriamae* seg. and *H. m. miriamae*
20. *Polites sabuleti genoa* and *P. s. tecumseh* (elevational)
21. *Pontia sisymbrii clevata* and *P. s. sisymbrii*
22. *Euchloe hyantis lotta* and *E. hyantis* ssp.
23. *Lycacna editha nevadensis* and *L. e. editha*
24. *Lycacna rubidus sirius* and *L. rubidus* ssp. (elevational)
25. *Satyrium fuliginosum semiluna* and *S. fuliginosum* ssp.
26. *Satyrium californica* seg. and *S. e. cygnus*
27. *Satyrium sylvinius* seg. and *S. s. sylvinius*
28. *Strymon melinus pudica* and *S. m. setonia*
29. *Glaucopsyche piasus nevada* or *G. p. toxema* and *G. p. piasus*
30. *Plebejus melissa melissa* and *P. m. fridajai* or *P. m. paradoxa* (elevational)
31. *Plebejus saepiolus saepiolus* and *P. saepiolus* seg. (elevational)
32. *Plebejus shasta minnehaha* and *P. s. shasta*
33. *Euphydryas editha monoensis* and *P. e. aurilacus* or *P. e. nubigena* (elevational)
34. *Euphydryas anicia wheeleri* and *E. a. veazieae* or *E. a. macyi*
35. *Cercyonis pegala* seg. and *C. p. stephensi*

BROAD ZONE OF ALLOPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

36. *Polites sonora utahensis* and *P. s. sonora*
37. *Speyeria cybele letona* and *S. e. leto*
38. *Speyeria egleis toyabe* and *S. e. egleis*
39. *Speyeria mormonia artonis* and *S. m. mormonia*

Table 4 continued.

40. *Euphydryas editha lehmani* and *E. e. monoensis*
41. *Coenonympha ochracea mono* and *C. ochraceae brenda*

ALLOCHRONIC SYMPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

42. *Euphilotes battoides baueri* and *E. b. glaucon*
43. *Euphilotes enoptes ancilla* and *E. e. enoptes*

pairs are narrowly sympatric, or nearly so, with little or no hybridization or intergradation in this zone. The closely related *Chlosyne palla* and *C. acastus* appear to be sympatric at the eastern base of the Sierra Nevada and in the Pine Nut and Virginia mountains without hybridizing. *Anthocharis sara thoosa* and *A. s. stella* co-occur in extreme western Nevada but with little intergradation (these, in fact, may be different species). Another species pair, *Limenitis weidemeyerii* and *L. lorquini*, hybridizes in a very narrow zone just east of the Sierra Nevada (Perkins and Perkins 1967) with extensions northward into Idaho and southwestern Alberta. Yet another pair, *Mitoura siva* and *M. nelsoni*, have long been considered distinct species. They, however, hybridize in a broad region in the western Great Basin and hence may be one species.

Isolated high-elevation populations of at least two species, *Polites sabuleti* and *Phyciodes campestris*, exist in the Sierra Nevada bounded on both the east and west by more widespread, lower-elevation subspecies. Two other species, *Euphydryas editha* and *E. chalcedona*, exist as a series of elevational subspecies (perhaps ecotypes) on the west slope to the crest of the Sierra Nevada and as a single middle-elevation subspecies on the east slope and into the western Great Basin. Numerous Great Basin subspecies (or segregates) are "replaced" by Sierra Nevada taxa between the western portion of the Great Basin and the crest of the Sierra Nevada (Table 4). There is usually narrow elevational allopatry and/or allochrony (imposed by elevational differences in phenology) between these phenotypes, but intergradation occurs in some. Furthermore, both *Euphilotes enoptes* and *E. battoides* are represented by sympatric allochronic "populations." These distinct univoltine populations fly at single locations at different times of the year and thus are reproductively isolated temporally (hence should constitute "allochronic species").



TABLE 5. Pairs of butterfly taxa showing various speciation phenomena in the northeastern Great Basin (most widespread Great Basin taxon listed first).

NARROW ZONE OF SYMPATRY BETWEEN CLOSELY RELATED SPECIES WITHOUT HYBRIDIZATION:

1. *Euphydryas anicia wheeleri* and *E. colon nevadensis*

NARROW ZONE OF SYMPATRY AND INTERSPECIFIC HYBRIDIZATION:

2. *Euphilotes enoptes ancilla* and *E. battoides glaucon*
3. *Coenonympha ochracea brenda* and *C. ampelos elko*

NARROW (USUALLY) ZONE OF SYMPATRY AND INTERGRADATION BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

4. *Colias alexandra edwardsii* and *C. a. astraea*
5. *Plebejus acmon acmon* and *P. a. lutzii*
6. *Speyeria nokomis apacheana* and *S. n. nokomis*
7. *Speyeria egleis utahensis* and *S. e. linda*
8. *Phyciodes campestris campestris* and *P. c. camillus*
9. *Euphydryas editha lehmani* and *E. e. hutchinsi*
10. *Limenitis archippus lahontani* and *L. a. archippus*

NARROW ZONE OF ALLOPATRY BETWEEN CLOSELY RELATED SPECIES:

11. *Papilio bairdii* and *P. oregonius* (may be conspecific)

NARROW ZONE OF ALLOPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

12. *Anthocharis sara thoosa* and *A. sara browningi*
13. *Satyrrium sylvinus* seg. and *S. s. putnami*
14. *Euphilotes rita pallescens* and *E. r. mattonii*
15. *Speyeria atlantis greyi* and *S. atlantis elko*

BROAD ZONE OF ALLOPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

16. *Satyrrium saepium provo* and *S. saepium* seg.
17. *Lycæna nivalis browni* and *L. n. nivalis*

Disjunctions between distinct species and between subspecies or segregates within the same species are manifest in both narrow and wide zones of allopatry in the Sierra Nevada Zone (Table 4). Some of these "gaps" are just a few miles wide, such as between the easternmost margin of the Sierra Nevada and the westernmost Great Basin mountain ranges. But other gaps include much of the broad expanse between the eastern Sierra Nevada and the mountains of central Nevada. Many species that range continuously across the region north of the Great Basin are also absent in this same broad area. Note that many gaps in distribution more or less coincide with regions of intergradation and of overlap between pairs of taxa discussed above.

#### Northeastern Nevada Zone

Another area of substantial apparent incipient speciation in the Great Basin is the northeastern portion of Nevada (Fig. 2). This area should probably include northwestern Utah,

TABLE 6. Pairs of butterflies taxa showing various speciation phenomena in central (C) and eastern (E) Great Basin (the most widespread Great Basin taxon is listed first).

NARROW ZONE OF SYMPATRY AND INTERSPECIFIC HYBRIDIZATION:

1. *Plebejus acmon texanus* and *P. lupini lupini* (C)

NARROW ZONE OF SYMPATRY AND INTERGRADATION BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

2. *Pontia sisymbrii elivata* and *P. sisymbrii* seg. (E, C)
3. *Satyrrium behrii crossii* and *S. b. behrii* (C)
4. *Celastrina ladon echo* and *C. l. cinerea* (C)
5. *Glaucopsyche piusis nevada* and *G. piusis daunia* (E)
6. *Plebejus acmon texanus* and *P. a. acmon* (C)
7. *Speyeria zerene gunderi* and *S. z. platina* (E)
8. *Phyciodes campestris campestris* and *P. c. camillus* (C)
9. *Limenitis weidemeyerii latifascia* and *L. w. angustifascia* (E)

NARROW ZONE OF ALLOPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

10. *Lycæna arota virginensis* and *L. a. schellbachi* (E)
11. *Euphilotes battoides baueri* and *E. battoides* seg. or *E. battoides* nr. *bernadino* (C)
12. *Euphilotes enoptes ancilla* and *E. enoptes* seg. (C)
13. *Plebejus saepiolus saepiolus* and *P. s. gertschi* (E) (elevational)
14. *Euphydryas editha lehmani* and *E. e. koreti* (E, C) (elevational)
15. *Neominois ridingsii stretchii* and *N. r. dionysus* (C)

southern Idaho, and southeastern Oregon, but for these latter areas few pertinent data exist. Information does exist for much of Elko and Humboldt counties and northern Eureka and Lander counties in Nevada. This area is considerably smaller in extent and lacks the abrupt topographical and ecological discontinuity of the Sierra Nevada–Great Basin interface. Nonetheless, some combination of factors there promotes differentiation and replacement. The region also marks the western or southernmost extent of the distributions of many species in the Great Basin (see below).

As in the Sierra Nevada Zone, there are replacements (specific and subspecific) with or without hybridization or intergradation and some, mostly narrow, allopatries (Table 5). While the zone of interaction along the Sierra Nevada is east/west in orientation, that in northeastern Nevada is more complicated (Fig. 2). The majority of interactions there involve east/west replacements of Rocky Mountain taxa with those of the Great Basin or Sierra Nevada. There are, however, several

TABLE 7. Pairs of butterfly taxa showing various speciation phenomena at the transition between the Great Basin and Mojave Desert (Great Basin taxon listed first).

NARROW ZONE OF SYMPATRY AND INTERGRADATION BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

1. *Pyrgus communis communis* and *P. c. albescens* (partial elevational allopatry, possibly different species)
2. *Hesperopsis libya lena* and *H. l. libya*
3. *Anthocharis cethura cethura* and *A. c. pima*
4. *Mitoura siva chalcosiva* and *M. s. rhodope*
5. *Glaucopsyche lygdamus oro* and *G. lygdamus* seg. (partial elevational allopatry)
6. *Euphydryas anicia wheeleri* and *E. a. alena*
7. *Cercyonis sthenele paulus* and *C. s. masoni*

NARROW ZONE OF ALLOPATRY BETWEEN CLOSELY RELATED SPECIES:

8. *Chlosyne acastus acastus* and *C. neumoegeni neumoegeni*

NARROW ZONE OF ALLOPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

9. *Polites sabuleti sabuleti* and *P. s. chusca*
10. *Papilio indra nevadensis* and *P. indra martini* or *P. indra* seg.
11. *Euphilotes battoides baueri* and *E. b. martini*
12. *Plebejus melissa melissa* and *P. melissa* seg.
13. *Apodemia mormo mormo* and *P. mormo* seg. (partial elevational and seasonal allopatry)

BROAD ZONE OF ALLOPATRY BETWEEN CLOSELY RELATED SPECIES:

14. *Chlosyne acastus acastus* and *C. palla vallismortis*

BROAD ZONE OF ALLOPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

15. *Plebejus icarioides ardea* and *P. icarioides* seg.
16. *Plebejus shasta minnehaha* and *P. s. charlestonensis*
17. *Speyeria zerene gunderi* or *S. z. malcolmi* and *S. z. carolae*
18. *Euphydryas anicia wheeleri* and *E. a. morandi*
19. *Limenitis archippus lahontani* and *L. a. obsoleta*
20. *Limenitis weidemeyerii latifascia* and *L. w. nevadae*

north/south replacements of taxa from Oregon or Idaho with generally widespread Great Basin taxa. One subspecies each of both *Speyeria egleis* and *S. atlantis* extends into this zone from the north and another from the east (Austin 1983). Furthermore, intergradation of phenotypes occurs among at least seven other subspecies pairs. For some of these (e.g., *Speyeria nokomis*, Swisher and Morrison 1969) this blending occurs over a broad area of the eastern Great Basin and northwestern Colorado; for others (e.g., *Euphydryas editha*) the cline is quite narrow. Finally, hybridization apparently occurs between *Euphilotes battoides* and *E. enoptes* (Shields 1977) and between the semispecies *Coenonympha ampelos* and *C. ochracea* of the *C. tullia* superspecies complex in this area.

### Eastern Nevada–Western Utah Zone

This region, which includes White Pine and Lincoln counties in Nevada and parts of adjacent Utah, is a comparatively minor area of speciation and faunal replacement (Table 6, Fig. 2). The apparent subspecific endemics are shown in Table 3. Most phenotypically identifiable replacements consist of Great Basin subspecies or segregate replacing Rocky Mountain subspecies with minor intergradation. There is, in addition, some replacement of desert subspecies or segregates with subspecies or segregates which range widely north of this zone. This portion of the Great Basin is most noteworthy as a northern or western limit of the distributions of a number of taxa (see below).

### Central Nevada Zone

This area includes the central Nevada mountains and valleys and is another comparatively minor area of interaction among phenotypes (Table 6, Fig. 2). Many of the interactions discussed for the previous two zones extend for varying distances into the Central Nevada Zone. Both east/west and north/south interactions are involved. A particularly interesting feature in this zone, and in other areas to the north as well, is the apparent hybridization between two species of blues, *Plebejus acmon* and *P. lupini* (Goodpasture 1973). The zone, in part, forms the eastern edge of a broad gap or zone of allopatry between species which are present between here and the Sierra Nevada (see above).

### Mojave Desert–Great Basin Zone

This area, including parts of Lincoln, Nye, and Esmeralda counties, Nevada, and Washington County, Utah, is recognized as the northern limit of Mojave Desert plants (Beatley 1975, Meyer 1978) and birds (Behle 1978, Johnson 1978), hence the southern limit of the Great Basin. Mammalian and herpetological distributions also support this as a distinct area of biological discontinuity (Hall 1946, Banta 1965a, b). Several butterfly species occurring widely in both areas exhibit different phenotypes on either side of this transition, while others intergrade across this area (Table 7, Fig. 2). There is a zone of allopatry for some taxa and segregates between the Great Basin and Mojave Desert, but this zone is generally

TABLE 8. Rocky Mountain butterfly species extending west to the Sierra Nevada across the Great Basin.

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<i>Hesperopsis libya</i>
<i>Hesperia uecas</i>
<i>Colias alexandra</i>
<i>Lycaena rubidus</i>
<i>Mitoura siva</i>
<i>Speyeria nokomis</i>
<i>Chlosyne acastus</i>
<i>Euphydryas anicia</i>
<i>Limenitis weidemeyerii</i>
<i>Coenonympha ochracea</i>
<i>Neominois ridingsii</i>

---

narrow. Only for *Limenitis archippus* is there a broad zone of allopatry; several hundred kilometers separate *L. a. obsoleta* in the Colorado River drainage and *L. a. lahontani* along the Humboldt River.

#### Wasatch Front Zone

The interface of the western escarpment of the Rocky Mountains with the Great Basin in central Utah superficially presents topographical and ecological contrasts comparable to that of the Sierra Nevada zone. Nevertheless, faunal replacement in this zone is not as striking as along the western edge of the Great Basin. Some endemic subspecies (or segregates) occur in this zone, and there is replacement of some Rocky Mountain taxa with those of the Great Basin. A sizable number of Rocky Mountain subspecies as discussed below, however, extend past this area well into the Great Basin. Widespread Great Basin butterflies such as *Hesperia comma harpalus*, *Pontia sisymbrii elivata*, *Euchloe hyantis lotta* (this taxon may be a species in itself, separate from *E. hyantis* fide P. A. Opler), *Lycaena rubidus sirius*, *Plebejus icarioides fulla*, *P. shasta minnehaha*, *Speyeria coronis snyderi*, and *S. calippe harmonia* range west from the Wasatch Front across virtually the entire Great Basin, some as far as the east slope of the Sierra Nevada.

#### DISTRIBUTIONAL LIMITS

Distributional limits of butterflies in the Great Basin and adjacent areas exhibit repeating patterns of particular interest. Some species, as mentioned, totally avoid the Great Basin, occurring solely at its borders. This overall situation essentially results from four distinct distribution patterns: (1) eastern taxa

that occur to the western limits of the Rocky Mountains, (2) extreme western taxa extending no further east than the east slope of the Sierra Nevada, (3) taxa of mainly Rocky Mountain affinity that occur to the eastern borders of the Great Basin, then north across Idaho and Oregon and, in numerous cases, south into the Sierra, and (4) southern taxa that occur north to southern Nevada and/or southwestern Utah.

Other species reach the limits of their ranges somewhere within the Great Basin region. This includes a number of butterfly taxa that enter only the eastern portion of the Great Basin and otherwise possess a distributional pattern like the species in (3) above. The limits of these latter two groups coincide closely with the zone boundaries discussed in the previous section on speciation.

Few Sierra Nevada species extend into the Great Basin and only *Plebejus lupini*, as mentioned above, for a substantial distance. The remainder occur, for the most part, only in the western Great Basin ranges. Of the two apparent endemic species of butterflies in the Sierra Nevada, *Hesperia miriamae* and *Colias behrii*, only *H. miriamae* extends its distribution into the Great Basin as a phenotypically distinct isolate found solely in the White Mountains. Endemic Sierra Nevada subspecies also have made few inroads into the Great Basin. Among the approximately 20 primarily alpine or subalpine taxa, only *Plebejus franklinii podarce* (one record from the Virginia Range) and *Polites sabuleti tecunseh*, *Chlosyne w. whitneyi*, and *Euphydryas editha nubigena* (Sweetwater Mountains) extend east into the Great Basin. The east slope of the Sierra Nevada, in turn, is the western distribution limit of at least 11 Rocky Mountain species (Table 8).

A number of Rocky Mountain species (some of which also occur in the Sierra Nevada) enter the Great Basin only in northeastern Nevada (Table 9). Most of these species have restricted Great Basin distributions and occur in both the Sierra and Rocky Mountains. Numerous additional species occur as isolates on many of the Great Basin ranges.

Three species with primarily southern distributions, *Hesperopsis alpheus*, *Anthocharis cethura*, *Philotiella speciosa*, occur throughout much of the western Great Basin but not the eastern. Several others extend to the east-



TABLE 9. Widespread butterfly species entering the Great Basin only in the northeastern portion.

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*Hesperia nevada*  
*Parnassius phoebus*  
*Papilio eurymedon*  
*Pieris napi*  
*Lycaena cupreus*  
*Lycaena dorcas*  
*Speyeria cybele*  
*Speyeria atlantis*  
*Speyeria mormonia*  
*Phyciodes tharos*

---

ern and central regions. None, however, reach northeastern Nevada except as strays or nonpermanent populations. A number of species reach their northern distributional limits in southern Nevada, south of the Mojave Desert/Great Basin transition (Austin and Austin 1980). Likewise, numerous Great Basin species have their southern distributional limits near that boundary. Nonetheless, more than 10% of the butterfly species in the Spring Mountains in extreme southern Nevada are of Great Basin affinity, and several endemic subspecies and segregates in this range appear to be closely related to Great Basin taxa (Austin 1981). This suggests a more extensive southern distribution for much of the Great Basin fauna in the past and agrees with our knowledge of the vicissitudes in Pleistocene climate (e.g., Martin and Mehlinger 1965, Wells 1983). Taxa with primarily northern distributions (e.g., alpine *Colias*, *Boloria*, *Erebia*, *Oeneis*), on the other hand, contribute very little in general to the Great Basin fauna. However, three putative "species," *Papilio oregonius*, *Euphydryas colon*, and *Coenonympha ampelos* (each conspecific with or siblings of more widespread Great Basin species), enter the northeastern region. One, *C. ampelos*, extends the furthest south, well into western Nevada to the Carson River basin.

#### PALLIDITY

At least 20 butterfly species exhibit their most pallid phenotype in the Great Basin (Table 10). An additional three butterfly subspecies groups reach their extreme in pallidity in the region. Linsdale (1938) and Hall (1946) noted a similar phenomenon in Nevada birds and mammals. Seven of the pallid butterfly

TABLE 10. List and general distribution of Great Basin pallid butterfly taxa.

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#### WESTERN GREAT BASIN

*Thorybes mexicana blanca*  
*Euphilotes rita* seg.  
*Speyeria zerene malcolmi* ("zerene" ssp. group)  
*Speyeria callippe nevadensis* ("nevadensis" ssp. group)  
*Coenonympha ochracea mono*  
*Cercyonis pegala stephensi*  
*Neominois ridingsii* seg.

#### CENTRAL GREAT BASIN

*Polites sabuleti* seg.  
*Speyeria egleis toyiabe*  
*Cercyonis octus pallescens*

#### NORTHEASTERN GREAT BASIN

*Ochlodes sylvanoides bonnevilla*  
*Lycaena editha nevadensis*  
*Speyeria atlantis greyi*  
*Speyeria atlantis elko* ("irene" ssp. group)  
*Speyeria mormonia artonis*  
*Phyciodes campestris* seg.  
*Coenonympha ampelos elko*

#### GENERAL GREAT BASIN

*Hesperia uncas lasus*  
*Incisalia eryphon* seg.  
*Speyeria nokomis apacheana*  
*Speyeria zerene gunderi*  
*Limnitis archippus lahontani*  
*Cercyonis sthenela paulus*

---

taxa and segregates are restricted to the northeastern region, seven are in western Nevada, three are in central Nevada, and six are more generally distributed. Some pallid subspecies and segregates are extremely restricted geographically, such as *Cercyonis oetus pallescens*, found only in small areas of the Reese River and Big Smoky valleys, and an undescribed *Euphilotes rita* segregate, found only at Sand Mountain east of Fallon. White alkaline or other pale soil was suggested as the key to predator-mediated selection for a pale ground color for many of these species (Emmel and Emmel 1969, 1971, Emmel and Mattoon 1972, Wielgus and Wielgus 1974). This may be true for some nondesert species as well (e.g., Hovanitz 1940, 1941, Bagdonas and Harrington 1979) and is supported by the presence of extreme dark phenotypes of some species in dark-background, marshy areas of the Great Basin (e.g., *Polites sabuleti* in eastern Nevada). The presence of pallid phenotypes in much of the Great Basin, of course, is also consistent with Watt's (1968) findings associating lighter basal wing color with warmer thermal regimes.



## DISCUSSION

The Great Basin butterfly fauna substantiates many zoogeographic generalities previously drawn for other taxonomic groups, particularly birds, in this region. Foremost, there is a general impoverishment of species richness inward from the peripheries, especially from the Rocky Mountains westward. This would be predicted from the similar distribution patterns recorded for plants (Billings 1978, Harper et al. 1978), in light of the close association of butterflies and their larval host plants. Nevertheless, suitable habitat (including adequate specific host plant availability) appears to exist for many butterfly species missing from portions of the Great Basin.

This impoverishment, as well as the previously noted endemism, presence of "relict" populations, and indications of recent extinctions (Austin 1985), is consistent with an "island effect" (MacArthur and Wilson 1967). This situation in the Great Basin largely arises from the sequestering of biotic diversity in comparatively small and isolated patches of montane habitat surrounded by sagebrush-dominated desert. The insular biogeography, particularly area effects and immigration-extinction dynamics, of the montane Great Basin mammals, birds, and butterflies has been discussed previously (Brown 1971, 1978, Austin 1981, Murphy and Wilcox 1985, Murphy et al. 1986, Wilcox et al. 1986). The same relationships are seen in fish and land snails (Smith 1978, Pratt 1985).

Montane or boreal biotic elements in the Great Basin appear to exhibit relictual distributions. This is best substantiated by mammalian distributions since they include both recent (Brown 1971, 1978) and fossil (Grayson 1982, 1983) evidence. These data indicate that present-day boreal mammalian faunas are not at equilibrium (that is, they lack balanced rates of extinction and of colonization) but are largely the result of range constriction and subsequent extinction (without recolonization) of a once widespread Pleistocene fauna. Fossil evidence from the central Great Basin reinforces the popular view that boreal habitat, extensive in the Pleistocene, withdrew northward and contracted toward montane summits. Grayson (1983) reports the fossil presence of the vole *Phenacomys* cf. *intermedius* in the Toquima Range. This species is

now restricted to areas far north and west of that range. Furthermore, pika (*Ochotona princeps*) remains have been recovered more than 1,000 m lower in elevation than known at present. Grayson (1982) implies that: (1) boreal mammals were widely distributed across the lowlands, (2) extinction led to the present absence of certain species on certain montane islands, (3) certain species became extinct on all montane islands, and (4) there was no Holocene recolonization.

For butterflies, we have only present-day distributions to examine. Butterflies, like birds, are considerably more vagile than most mammals; thus, it is not surprising that they show less-dramatic effects of island size and isolation. That butterflies are more mobile than mammals (but less so than birds) is reflected in the comparatively low slope associated with the species-area curves for butterflies from Great Basin mountain ranges (Murphy et al. 1986, Wilcox et al. 1986). Hence, rates of interrange (interisland) dispersal should be higher, and recolonization after extinction more frequent, in butterflies than in mammals. Nonetheless, a significant area effect is found for butterflies. But, supporting the notion that rates of extinction exceed that of colonization in at least some butterfly species, Wilcox et al. (1986) have shown that the numbers of "sedentary" butterfly species are better correlated with area than are "vagile" butterflies. Less-mobile taxa (e.g., montane land snails and lowland fish) exhibit an even greater effect of isolation and extinction in this region (Smith 1978, Pratt 1985).

Note that islandlike effects of area and isolation are not restricted to montane or boreal elements in the Great Basin. Lowland riparian butterflies appear to be equally isolated, and the faunas of these communities exhibit similar effects (Austin 1985). Riparian butterfly species richness decreases from the Colorado River Valley northward (upstream) into the central Great Basin. In the northern Great Basin, species richness decreases from the relatively rich upper river valleys (Humboldt, Carson, Walker) downstream toward the central Great Basin.

Given the high number of phenetically distinct, geographically restricted endemic butterfly subspecies and segregates, it is of interest to note patterns of differentiation in other

taxa within the Great Basin. Speciation in all taxa is most striking along the western and northeastern edges of the Great Basin. But, differentiation certainly is not limited to these areas. Stutz (1978), for instance, identified several rich evolutionary sites for *Atriplex* in the Great Basin, similar to those found for birds (Behle 1963, Johnson 1978), and corresponding to centers of differentiation and limits of distributions of plants in the Great Basin as outlined by Cronquist et al. (1972). These studies and our butterfly data clearly indicate the existence of distinct areas of interaction and speciation within the whole of the Great Basin.

As we mentioned in several sections above, butterflies and birds are extremely similar in their patterns of distribution and differentiation within the Great Basin. This similarity also extends to other taxa including reptiles and amphibians (Stebbins 1954) and mammals (Hall 1946, Hall and Kelson 1959). *Ambystoma tigrinum* and *Bufo woodhousei* are Rocky Mountain amphibian species not occurring in the Great Basin but extending west along its northern margin. A far-western Great Basin subspecies of *Bufo boreas* replaces a widespread interior subspecies in the western Great Basin, and an isolated subspecies occurs in the Inyo Region. Reptiles that avoid the Great Basin but occur along its borders include *Phrynosoma douglasii* and *Thamnophis sirtalis*, the latter occurring in both the Rocky Mountains and the Sierra Nevada. Subspecific intergradation occurs along the Sierra Nevada–Great Basin interface (*Sceloporus graciosus*, *S. occidentalis*, *Thamnophis elegans*, *Crotalus viridus*) and near the Mojave Desert–Great Basin transition (*Callisaurus draconoides*, *Phrynosoma platyrhinos*, *Uta stansburiana*). Extension of primarily southern species northward in the western Great Basin east of the Sierra Nevada is relatively common. Tanner (1978) commented on the absence in the Great Basin of expected montane species or of endemic species of amphibians and reptiles.

Numerous examples of similar phenomena exist among mammals. Species such as *Lepus americanus*, *Eutamias amoenus*, *Tamiasciurus douglasii*, and *Martes americana* are found in both the Rocky Mountains and Sierra Nevada but not the Great Basin. Others extend northward from the southern deserts only in the western Great Basin. An interface

exists between subspecies in the extreme southern or extreme western Great Basin for several mammal species. Subspecific endemics largely follow the patterns described above for butterflies. One species, *Microdipodops pallidus*, in fact, is a Great Basin endemic. The distributions of mammals at the species level (Hagmeier 1966) are consistent with our butterfly data; and more fine-grained, below-the-species-level studies may well further strengthen this comparison with our findings.

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